

Studies on the Charopidae of tropical and subtropical Australia. I. *Oreokera*: A primitive genus from the high mountains of North Queensland (Mollusca : Pulmonata : Charopidae)

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ABSTRACT

The charopid genus *Oreokera* is shown to be an invalidly introduced taxon. It is herein formally validated and redefined. The genus contains two species found only on the summits of the high mountains of north-east Queensland. The type species, *Oreokera cumulus* (Odhner, 1917) is redescribed and refigured on the basis of newly dissected topotypic material. A new species, *Oreokera nimbus* from Thornton Peak, is figured and described. *Oreokera* is identified as a primitive taxon among the Charopidae by the absence of a closed secondary ureter in either *O. cumulus* or *O. nimbus*. The relationships of the genus are discussed and some comments made on its biogeographic status.

INTRODUCTION

The Australian Charopidae has traditionally been viewed as a group which shows its greatest diversity in the cool temperate forests of south-east Australia. However, recent collecting in Queensland and northern New South Wales has revealed a remarkable radiation in the sub-tropical and tropical rainforests. Particularly significant is the charopid diversity shown by the group on the high mountains of north east Queensland. The Charopidae, as a widespread and ancient group, has the potential to provide significant data on the biogeography of this area, but a primary barrier to the initiation of these studies has been lack of material. Until recently, knowledge of the molluscan fauna on these peaks rested with a species list (10) prepared by Charles Hedley (1889) after an early expedition up Mt Bellenden Ker (Meston, 1889) and several sporadic collections including the 1910-1913 Swedish Scientific Expedition.

In 1981 an expedition by Queensland Museum staff and volunteers, sponsored by the American-based Earthwatch organisation, collected 46 species of terrestrial mollusc from Mt Bellenden Ker. Of these, 22 species were collected from the summit, including 10 species not found at altitudes lower than 1000m. These results indicated a strong altitudinal stratification among the land snails similar to that shown by the plants and insects. Most notable from a biogeographical viewpoint

however, was the large number of charopids — 10 species, of which 6 did not occur under 1000m (Stanisci, unpublished). Only one, *Oreokera cumulus* (Odhner, 1917), had been previously described.

SYSTEMATIC REVIEW

The following treatment of *Oreokera* is based on the limited amount of material in the Queensland Museum (QMMO) and Australian Museum, Sydney (AMC). Although Nils Odhner described '*Flammulina' cumulus* in 1917, further additions to the material available for study have been made only recently and largely through the efforts of entomologist Dr Geoff Monteith. While this has enabled an adequate description of *Oreokera cumulus* (Odhner, 1917) and *O. nimbus*, material is still limited.

Oreokera, has a disjunct distribution on the mountains and plateaux above 1000 metres in the tropical rainforest region of north-east Queensland (Fig. 1), *O. cumulus* is the more widespread, occurring on several peaks from Mt Bartle-Frere in the south to Devil's Thumb, south-east of Mossman in the north. *O. nimbus* has been found only on Thornton Peak, north of the Daintree River. Both species are confined to altitudes above 1000m where rainfall is high and the forest types are environmentally similar to the temperate forests of southern Australia.

GENUS OREOKERA NEW GENUS

Oreokera Iredale, 1933, Records Australian Mus., 19(1): 54; Iredale, 1937, Australian Zool, 8(4): 318; Iredale, 1941, Australian Nat., 10(8): 264 — nude names.

Diagnosis

Shell medium to large, spire moderately to strongly elevated. Apical whorls with prominent spiral cords, fewer and more regular in *cumulus* (Plate 1a-b) than *nimbus* (Plate 2a-b), with a secondary sculpture of vague radial rugosities on the last portion (Plate 1a). Post apical sculpture complex, of regularly spaced, very prominent radial ribs with well developed periostracal blades (Plate 2c). Microsculpture of prominent radial riblets crossed by finer microspirial cordlets, more numerous in *cumulus* than *nimbus* (Plates 1c-d, 2d-e). Sculpture not reduced below periphery and continuous on base (Plate 2f). Periphery acutely rounded to keeled (Plate 2b,e). Body whorl not descending. Lip simple with well developed parietal callus. Shell colour yellow-horn to brown with darker flammulations above and below (Figs 2a,c,d,f). Genitalia with bilobed ovotestis oriented at right angles to plan of coiling, strongly kinked hermaphroditic duct, talon and carrefour without unusual features (Figs 3d, 4b, 4d, 5b, 5c, 5e). Albumen gland, prostate and uterus typical (Fig. 3b,d). Penis moderately (*cumulus*) to strongly (*nimbus*) swollen (Figs 3c, 5a), internally with complex (*nimbus*) to simple (*cumulus*) pilasters (figs 4a, 5d). Epiphallus well developed, reflexed, with accessory caecum and moderately long (*nimbus*) to very long (*cumulus*) flagellum entering penis through a verge (*nimbus*) or simple pore (*cumulus*) (Figs 3c, 5a). Penial retractor muscle short, inserting on the epiphallal caecum (Fig. 5d). Vas deferens a simple tube (Figs 3c, 5b). Spermatheca typical. Free oviduct short, almost as long as vagina. Vagina and atrium short (Figs 3a, 5a), internally with longitudinal pilasters. Pallial cavity with no secondary ureter, kidney with much reduced rectal lobe and prominent pericardial lobe (Figs 4c, 5f). Pallial roof pigmented, with slight intrusion of mantle gland. Animal darkly pigmented above. Radula with tricuspid central tooth that has the mesocone almost twice the length of the endocone and ectocone. Inner laterals similar, lateromarginals with mesocone reduced and endocone split. Marginals with complex endo- and ectoconal cusps, mesocone reduced (Plate 2e-f).

Type Species: *Flammulina cumulus* Odhner, 1917

Comparisons

The extremely prominent radial ribs, keel, elevated spire, almost closed umbilicus, apical spiral cords and strongly reticulate postnuclear microsculpture of *Oreokera* are a combination of shell characters not found in any other north-east Queensland charopid. *Mussonula* Iredale, 1937 from south-east Queensland, has a narrowed umbilicus, strongly radial sculpture on the post apical

whorls, elevated spire and spirally striate protoconch, but lacks the flammulations and post nuclear microsculpture of *Oreokera* and is less than half the size. *Hedleyoconcha* Pilsbry, 1893 from northern New South Wales and southern Queensland has an elevated spire and almost closed umbilicus but differs in having reduced post apical sculpture of low radials and low broad spirals as well as a pustulose protoconch.

The main features characterising *Oreokera* are in its anatomy. The absence of a secondary ureter, kinked hermaphroditic duct, orientation of the ovotestis and accessory appendages on the male genitalia are basic departures from the charopid patterns discussed by Solem (1983). While some of these may be secondary modifications associated with the arboreal lifestyle and altered shell shape of *Oreokera*, the absence of a secondary ureter identifies it as a primitive taxon among the Charopidae. The posteriorly opening ureter (Figs 4c, 5f) is typical among the Pacific Island Endodontidae. Solem (1976, pp. 84-87) discussed the significance of the closed ureter in the Charopidae and considered this a major advance over the incomplete or absent secondary ureter.

Key to the Species of *Oreokera*

1. Spiral cords on protoconch mainly regular, diameter of protoconch 885µm at 1½ whorls; adult microsculpture with microspirals less widely spaced than radial riblets; penis interior with main pilaster, no verge; epiphallic flagellum long, 4 times length of penis (Figs 2a-c, 3a-d, 4a-d, Plate 1a-f).....*Oreokera cumulus* (Odhner, 1917)
2. Spiral cords on protoconch mainly squiggly, diameter of protoconch 1065µm at 1½ whorls; adult microsculpture with microspirals equally or more widely spaced than radial riblets; penis interior with complex pilasters, verge present; epiphallic caecum short, 2 times length of penis (Figs 2d-f, 5a-f, Plate 2a-f).....*Oreokera nimbus* sp. nov.

Nomenclature and Previous Studies

Iredale (1933) introduced the taxon *Oreokera* as follows: "As the species (referring to *F. cumulus*) is certainly not conchologically referable to the genus *Flammulina*, the new genus *Oreokera* is proposed for it." Solem (1964, p. 46; 1979, pp. 46, 92) and Smith and Kershaw (1985, pp. 1-2) have justifiably argued that a number of taxa introduced in that publication (Iredale, 1933) were *nomina nuda* because of little or no accompanying description. For similar reasons Iredale's introduction of *Oreokera* is considered invalid. In some instances Iredale subsequently validated these poorly proposed taxa. However, this was not the case with *Oreokera* which only appeared as an entry in his later check list (Iredale, 1937 p. 318). In order to maintain consistency with the views of the above authors, the name *Oreokera* is retained but herein validated.

Odhner (1917) assigned *O. cumulus* to the New Zealand genus *Flammulina* Martens, 1873 and near to *Helix corticicola* Cox, 1866 from southern Queensland on the basis of overall conchological similarity. Iredale (1933) on the basis of the reasons given above, rejected Odhner's association, considered that these two species deserved separate generic recognition and invalidly introduced the taxon *Oreokera* to accommodate them. Rather fortuitously the present study shows Iredale to be partly correct in that *Flammulina* shows major differences in pallial and genital anatomy which suggest that any conchological consistencies with *Oreokera* are convergent (See Solem, 1983, p. 64, fig. 29).

It is highly doubtful if Iredale ever viewed the type or any other specimen of *O. cumulus*. It is, however, more probable that his association of *H. corticicola* with the Bellenden Ker species was based solely on Odhner's earlier assessment. Besides anatomical differences (Stanisic, unpublished) there are major conchological differences between these two species. *H. corticicola* has a radially sculptured protoconch, less intricate microsculpture and quite different coiling pattern to *O. cumulus*. *Oreokera dorriagoensis* Iredale, 1941 was included here by Iredale on the basis of its similarity to *H. corticicola*. While these two latter species show acceptable generic level similarity to each other, they are excluded from *Oreokera* as herein defined and will be discussed elsewhere.

Distribution and Basic Ecology

Oreokera ranges from Mt Bartle-Frere at the southern end of the Bellenden Ker Range to Thornton Peak in the north. In between it occurs at Mt Bellenden Ker, Devil's Thumb (near Mossman), Mt Lewis and Black Mountain (near Julatten). There are no records from the Atherton Tableland, Graham Range, Windsor Tableland or the more northerly peaks of the Daintree to Bloomfield rainforest. It is restricted to the simple microphyll vine fern forests and thickets occurring on these peaks, at altitudes near or above 1000m.

Collecting efforts in the Atherton Tableland and Graham Range have been sufficient to indicate that its absence from these areas is real. There is still hope of finding *Oreokera* at localities such as Mt Spurgeon (alt. 1341m) and Mt Finnegan (alt. 1148m). The disjunct, restricted distribution of *Oreokera* is at first glance remarkable, but has a number of counterparts in plant and other invertebrate groups and its significance will be discussed further below.

Oreokera has been collected in arboreal ('axils of palm fronds') and semi-arboreal ('under bark of rotting logs') situations. It has not yet been found live in the litter.

OREOKERA CUMULUS (ODHNER, 1917) (Plate 1a-f; Figs 2a-c, 3a-d, 4a-d)

Flammulina cumululus Odhner, 1917, Kungl. svensk. Vetens. Handl., 52(16): 84, pl. 3. figs 89-91 — Mt Bellenden Ker, NE Queensland, 4000ft.

Oreokera cumululus (Odhner), Iredale, 1933, Records Australian Mus., 19: 54; Iredale, 1937, Australian Zool., 8(4): 318.

Comparative Remarks

Oreokera cumululus (Odhner, 1917) is recognisable by its almost closed umbilicus, flammulated shell with strong radial sculpture (figs a-c), relatively large size (mean diameter 6.64mm), elevated spire (mean H/D ratio 0.67) with spirally striate protoconch (Plate 1a), and its range south of the Daintree River (Fig. 1).

Oreokera cumululus is larger and has a greater mean whorl count than *O. nimbus* but differs most obviously in having fewer and more regular apical cords and more crowded microspirals on the postnuclear whorls (Plate 1a, 1c). Genital differences include a longer epiphallallic flagellum, simple penial pilaster pattern and the absence of a verge in *O. cumululus* (Figs 3c, 4a). These features contrast with the shortened flagellum, more complex penial pilasters and prominent penial verge found in *O. nimbus* (Figs 5a, 5d).

TABLE 1: Local variation in *Oreokera cumululus* (Odhner, 1917)

LOCALITY	NUMBER OF ADULTS MEASURED	RIBS ON BODY WHORL	RIBS PER MM	HEIGHT (MM)	DIAMETER (MM)	H/D	WHORLS
Mt Bellenden Ker QMMO. 14765	1	49	2.21	5.19	7.06	0.74	5¼
Devil's Thumb QMMO. 15444	1	76	4.31	3.57	5.62	0.64	4¾
Black Mtn. QMMO. 15430 AMC.149591	5	74.2 (70-83)	3.50 (3.12-3.93)	4.48 (4.34-4.60)	6.76 (6.30-7.15)	0.66 (0.62-0.69)	4⅞+ (4¾-5)

Holotype

Naturhistoriska Riksmuseet, Stockholm, E. Mjoberg, May, 1913. (1 live specimen).

Material Studied

North East Queensland:

Mt Bellenden Ker, summit, 1560m, SMVFT (1 specimen, QMMO.11274, 1-7 Nov. 1981, Earthwatch/QM); Mt Lewis Road, via Julatten (1 specimen, QMMO.16126, 12 Oct. 1980, G.B. Monteith); Mt Lewis, ca 17.8km along Julatten — Mt Lewis Road, litter, MVFF (1 specimen QMMO.14760, 27 Jun. 1983, J. Stanisic, D. Potter); Leichhardt Ck crossing on Mt Lewis Road, Mt Lewis, litter, SMVFF (1 specimen, QMMO.14756, 1 Oct 1980, J. Stanisic); Black Mountain, 17km ESE of Julatten, 800-1000m (6 specimens, AMC.149591, QMMO.15430 29-30 Apr. 1982, G.B. Monteith, D. Yeates, D. Cook); Mt Bellenden Ker, Summit, 1560m, beating foliage, (1 specimen, QMMO.14765, 1-7 Nov. 1981, Earthwatch/QM); Mt Bartle-Frere, NW-Centre Peak Ridge, 1400-1500m (1 specimen, QMMO.16125, 7-8 Nov. 1981, Earthwatch/QM); Mt Lewis, summit, 1200m (2 specimens, QMMO.15427, 9 Sept. 1981, G.B. Monteith, D. Cook); Mt Lewis, summit, 1200m, rainforest, stick brushings (1 specimen, QMMO.15433, 10 Sept. 1981, G.B. Monteith, D. Cook); Devil's Thumb area, 10km NW Mossman, rainforest (2 specimens, QMMO.15444, 9-10 Oct. 1982, G.B. Monteith, D. Yeates, G. Thompson); Mt Bellenden Ker, just below summit, approx. 1500m, under bark of rotting log, SMVFT (7 specimens, QMMO.14876, 4 Jul. 1983, J. Stanisic, D. Potter); Mt Bellenden Ker, summit TV stn, 1560m, SMVFT (1 specimen, QMMO.11262, 25-31 Oct. 1981, Earthwatch/QM); Mt Bellenden Ker, summit TV stn, 1560m, SMVFT, in axils of palm fronds (2 specimens, QMMO.11253, 17-24 Oct. 1981, Earthwatch/QM).

Diagnosis

Shell large, diameter 5.62-7.15mm (mean 6.46mm), with 4 3/4 — 5 1/4 (mean 5-) normally coiled whorls. Apex and spire moderately to strongly elevated, body whorl not descending, spire protrusion about 2/5 body whorl width (Figs 2a-c). Height of shell 3.57-5.19mm (mean 4.35mm), H/D ratio 0.62-0.74 (mean 0.67). Apical sculpture of 17-20 prominent, narrow spiral cords. Protoconch of 1 3/4 whorls, 855µm in diameter at 1 1/2 whorls (Plate 1a-b). Post-nuclear whorls with widely spaced, strongly protractively sinuated radial ribs (Plate 1a), 49-83 (mean 70.9) on body whorl, whose interstices are 8-12 times their width. Ribs/mm 2.21-4.31 (mean 3.43). Microsculpture of numerous fine radial riblets, 6-10 between each pair of major ribs, crossed by fine, more closely spaced spiral cords (Plate 1c-d). Umbilicus narrow, reduced to a small chink in some individuals (Fig. 2c). Sutures simple. Whorls rounded above and below a broadly keeled periphery (Fig. 2b). Aperture sub-ovate, inclined about 25° from shell axis. Lip simple, parietal callus well developed (Fig. 2e). Colour yellow-horn to brown, with prominent (rarely reduced), red-brown flammulations, persisting on the base (Fig. 2a, c).

Description of Soft Parts — Foot and tail broad, bluntly rounded posteriorly, not tapering. Sole undivided, with strong transverse corrugations extending up the sides of the foot to the pedal groove. Pedal grooves high on foot, distinct, upper less prominent, uniting over tail. No mid-dorsal groove or caudal horn. Slime network well developed, irregular oblong to rectangular.

Body colour (in preservative) yellowy-brown, with pedal grooves, head region, mantle collar, posterior dorsal and lateral areas of foot covered by varying degrees of black pigmentation. Pallial roof with an arc of black pigmentation in heart region and variable spotting on left side behind the mantle collar. Ommatophores black.

Mantle collar (MC) thick, well developed, darkly pigmented in some specimens, glandular extension (MG) protruding onto anterior edge of pallial roof. Pneumostome (LP) obscured by mantle lobe (MA). Anus and pneumostome (LP) sharing a common opening to exterior. Anus opening just posterior to mantle collar with a narrow groove angling to exterior edge of mantle collar (Fig. 4c).

Pallial region long (almost 7/8 whorl apically), anterior edge with intrusive mantle gland (MG). Lung roof with varying degrees of black pigmentation, most notable overlying renal arm of the ureter (KD) and just posterior to mantle gland. Kidney (K) short, pericardial lobe vaguely triangular, rounded anteriorly and much longer than rectal lobe. Rectal lobe small, overlying hindgut (HG). Ureter (KD) sigmurethrous, secondary ureter absent. Ureteric opening (KX) just anterior to rectal arm of kidney. Heart (H) about 2/3 length of kidney. Principal pulmonary vein (HV) following contour of kidney to apex, then angled toward pneumostome, without conspicuous branches (Fig. 4c).

Ovotestis (G) embedded in apical coils of digestive gland, consisting of two clumps of palmately clavate alveoli orientated at right angles to plane of coiling (Fig. 4d). Apical clump variously sub branched. Clumps may be subdivided by digestive gland. Hermaphroditic duct (GD) large, swollen, iridescent pink and convoluted, sharply tapering at either end (Fig. 3d). Carrefour (X) a noticeable swelling at the base of the talon shaft, receiving a thin duct (Fig. 4b) from the ovotestis, a larger duct from the albumen gland (GG) and the slightly swollen stalk of the talon (GT). Talon a conspicuous swelling, embedded in the surface of albumen gland with a short, stout stalk which reflexes to enter the carrefour region (Figs. 3d, 4b). Prostate (DG) consisting of numerous acini, attached to one side of the uterus (UT) as a thin sheet for its entire length, then expanding into a bulbous mass at the level of the spermathecal head (Fig. 3d). Prostatic channel a lateral outpocket of the uterine lumen. Uterus (UT) superficially differentiated into two lower thick walled chambers and a thin walled upper chamber. Medial chamber brown in colour.

Vas deferens (VD) initially thickened then narrowed (Figs. 3a, 3c), descending vagina (V) to penioviducal angle, ascending penis (P) and entering epiphallus (E) at the level of the epiphallic caecum (ERC). Vas deferens — epiphallus region internally with simple longitudinal thickenings. Epiphallus with ascending and descending branches and very long (almost 4 times length of penis) epiphallic flagellum (EF) arising at the point of flexure and a short caecum (ERC) situated about ½ way along descending branch (Fig. 3c). Internally epiphallic caecum with walls thrown into folds, epiphallic flagellum with corrugated longitudinal pilasters. Epiphallus entering penis through a thickened pilaster (PV). Penis simple, muscularised tube, internally (Fig. 4a) with apical transverse pilasters (PP), longitudinal corrugated pilasters (PP), and a large central pilaster (PPM). Penial retractor muscle (PRM) short, inserted on the epiphallic caecum. Atrium (Y) short with longitudinal pilasters.

Free oviduct (UV) straight, long, almost equal in length to vagina. Vagina (V), internally with fleshy longitudinal pilasters, externally with prominent connective tissue (Fig. 3a). Spermatheca with a basal muscular portion, long convoluted stalk (SS) overlying uterus (Fig. 3a), and terminating in a sub-ovate shaped head (S) which lies in an area between the prostate and the albumen gland. Albumen gland (GG) a small roughly rounded mass of acini (Fig. 3b, d). (Based on 3 dissected specimens, QMMO.14876, QMMO.11253).

Remarks

Oreokera cumulus (Odhner, 1917) has a disjunct distribution on the summits of the high peaks south of the Daintree River to Mt Bartle-Frere (Fig. 1). The distribution is unusual but can be related to recent regressions of rainforest habitat in the region caused by climatic change. The less elevated spire and subtle differences in shell features of the Black Mountain specimens would indicate that a study of interpopulational variation may be worthwhile in trying to understand possible speciation trends with the genus.

O. cumulus has a quite simple pattern of penial pilasters when compared with the actively speciating Pacific Island charopids. This may be related to its existence under fairly stable environmental conditions over a long period of time or a lack of sympatric relatives.

OREOKERA NIMBUS SP. NOV.

Plate 2a-f; Figs 2d-f, 5a-f

Comparative Remarks

Oreokera nimbus has a larger protoconch (1065µm at 1½ whorls) with more numerous and more closely spaced spiral striae than *O. cumulus*. In addition, the apical striae in *O. nimbus* are more 'squiggly' than in *O. cumulus* (Figs 2d-f, Plate 2a-b). Lack of adequate material does not make it possible to comment on differences in shape and coiling patterns between the two species. However, there are noticeable differences in the postnuclear microsculpture. The adult microsculpture of *O. nimbus* has the microspirals spaced as wide or wider than the radial riblets (Plate 2d) whereas in *O. cumulus* the microspirals are more closely spaced than the microradials (Plate 1c). Anatomically *O. nimbus* differs from *O. cumulus* in having a smaller epiphallic flagellum, more muscular and swollen penis with more complex internal pilasters, and a penial verge (Fig. 5a, 5d). The animal of *O. nimbus* appeared to be more darkly pigmented than *O. cumulus*, however, this may be individual rather than specific variation.

Holotype

QMMO. 16302, Thornton Peak, 11km NE Daintree, NEQ. Collected by G.B. Monteith, D. Yeates and G. Thompson 30 October, 1983. Height of shell 4.34mm, diameter 6.55mm, H/D ratio 0.66, whorls 4¾+.

Paratypes

Thornton Peak, 11km NE Daintree, NEQ, 1100-1200m (5 adults, 7 sub-adults and juveniles, QMMO. 15438, AMC.149590, 30 October, 1983, G.B. Monteith, D. Yeates, G. Thompson); Thornton Peak, NEQ, 1100-1300m (2 adults, 6 sub-adults and juveniles, QMMO.15170, 24-27 September, 1981, G.B. Monteith).

Other Material

Thornton Peak, NEQ, 1000-1300m (2 sub-adults, QMMO.15445, 20-22 September, 1981, G.B. Monteith, D. Cook); Thornton Peak, NEQ, summit, 1100-1300m, rainforest, sieved litter and moss (1 sub-adult and 1 juvenile, QMMO.16304, 24-27 September, 1984, G.B. & S.R. Monteith).

Diagnosis

Shell large, 5.62-6.55mm (mean 6.08mm) in diameter, with 4½-5⅙+ (mean 4¾+) normally coiled whorls. Apex and spire strongly elevated, body whorl not descending (Fig. 2d-f). Height of shell 3.92-4.43mm (mean 4.26mm), H/D ratio 0.66-0.75 (mean 0.70). Apical sculpture of 24-30 prominent spiral cords which are initially regular then becoming noticeably squiggly or zig-zagged (Plate 2b). Protoconch of 1¼ whorls, 1065µm in diameter at 1½ whorls (Plate 2a). Postapical whorls with widely spaced, strongly protractively sinuated radial ribs, 54-73 (mean 63) on body whorl, whose interstices are 8-12 times their width (Plate 2c). Major ribs with well developed periostracal blades. Ribs/mm 2.92-3.79 (mean 3.28). Microsculpture of numerous fine radial riblets, 6-13 between each pair of major ribs, crossed by fine, more widely spaced spiral cords (Plate 2d). Sculpture not reduced below periphery and continued on base (Plate 2f). Umbilicus narrow, reduced to a lateral crack in some individuals (Fig. 2f). Sutures simple. Periphery broadly keeled (Fig. 2e). Aperture sub-ovate inclined about 25° from shell axis. Lip simple, parietal callus well developed. Colour brown with prominent red-brown flammulations, persisting on base (Fig. 2d, 2f). Based on 7 measured adults.

Description of Soft Parts — Foot and tail broad, bluntly rounded posteriorly. Sole undivided with very strong transverse corrugations extending up the sides of the foot to the pedal groove. Pedal grooves high on foot, distinct, upper less prominent, uniting over tail. No mid-dorsal groove or caudal horn. Slime network well developed, irregularly oblong to rectangular.

Body colour (in preservative) yellowy-white, with pedal glands, head region, mantle collar, posterior dorsal and lateral areas of foot, distinctively dark grey to black. Pallial roof with a large area of black pigmentation. Ommatophores black.

Mantle collar (MC) not as well developed as in *O. cumulus*, with mantle gland (MG) only slightly intruding onto pallial roof. Pneumostome (LP) obscured by mantle lobe (MA). Anus and pneumostome sharing a common opening to the exterior. Anus opening just posterior to mantle collar (Fig. 5f).

Pallial region contracted, anterior edge with slight intrusion of mantle gland (MG). Lung roof with a large area of black pigmentation in the anterior half. Kidney (K) short, pericardial lobe vaguely triangular, reflexed away from the rectum (HG), rounded anteriorly and much longer than rectal lobe. Rectal arm of kidney reduced to a small knob of tissue overlaying rectum (HG). Ureter (KD) sigmurethrous, without secondary branch. Ureteric opening (KX) just anterior to rectal kidney arm. Heart (H) about ⅓ length of kidney, principal pulmonary vein (HV) not branched (Fig. 5f).

Ovotestis (G), two clumps of palmately clavate, white alveoli, embedded in the pink apical whorls of the digestive gland (Z). Apical clump larger and separated from subapical clump by digestive gland tissue (Fig. 5e). Hermaphroditic duct (GD), light iridescent pink and strongly kinked (Fig. 5c). Carrefour (X) not seen. Talon (GT) a subcircular swelling embedded in the surface of the digestive gland, with a short stout stalk which reflexes to enter the carrefour region (Fig. 5b). Prostate (DG) white, consisting of numerous acini arranged as a thin sheet of tissue on the lower uterine chamber, expanding into a bulbous mass at the level of the albumen gland (GG). Uterus (UT)

too flattened to observe differentiation, central region brown in colour. Albumen gland, a roughly rounded mass of acini, deformed by contraction. Spermatheca (S) with a muscularised basal portion (Fig. 5a), gradually tapering to a thin stalk (SS), terminating in a sub-ovate head lying at the base of the albumen gland.

Vas deferens (VD) initially thickened then descending to penioviducal angle, ascending penis (P) and entering epiphallus at the level of the epiphallal caecum (ERC). Epiphallus (E) reflexed, with ascending and descending branches (Fig. 5a). Long (about 2 times length of penis) epiphallal flagellum (EF) arising at the point of flexure. Small epiphallal caecum (ERC) about midway along descending section of epiphallus (Fig. 5a). Penial retractor muscle (PRM) very short, inserting on the caecum (Fig. 5b, 5d).

Epiphallus, vas deferens and flagellum internally with longitudinal pilasters. Penis (P) muscularised and swollen apically, internally (Fig. 5d) with large, corrugated longitudinal pilaster (PPM), a pocket stimulator (PPS) and wall sculpture of low corrugated pilasters (PP). Epiphallus (Fig. 5d) enters penis apically through two thickened pilasters which function as a verge (PV). Apicad of verge, epiphallus with two large thickened longitudinal pilasters (EPP).

Free oviduct (UV) short (Fig. 5a), contracted, almost as long as vagina (V). Vagina internally with thin, longitudinal pilasters, externally with pigmented connective tissue (Fig. 5a). Atrium (Y) short with internal longitudinal pilasters. Based on one dissected adult. (QMMO.15438).

TABLE 2. Variation in *Oreokera nimbus*

LOCALITY	NUMBER OF ADULTS MEASURED	RIBS ON BODY WHORL	RIBS PER MM	HEIGHT (MM)	DIAMETER (MM)	H/D	WHORLS
Thornton Peak	7	63	3.28	4.26	6.08	0.70	4¾+
QMMO.16302		(54-	(2.92-	(3.92-	(5.62-	(0.66-	(4½-
QMMO.15438		73)	3.79)	4.43)	6.55)	0.75)	5⅛+)
AMC.149590							

Remarks

Oreokera nimbus is known only from the summit (alt. approx. 1000m) of Thornton Peak (Fig. 1). Even though the geographic distance is no greater than that shown by the north-south range of *O. cumulus*, it has not been found on neighbouring Mt Hemmant (1092m) and Mt Pieter Boite (1046m) or the more northerly Mt Finnegan (1148m).

Monteith (1985) noted that the Mt Sorrow Tableland which includes the slopes of Mt Pieter Boite, lacked many of the insect taxa found on the Bellenden Ker Range. However, it did contain some relict endemic taxa. He suggested that while these facts established the area as a refuge zone, it may have been less significant than some of the higher massifs in the south. Hence, the absence of *Oreokera* on some of the more northern peaks of the Daintree-Helenvale rainforest may in fact be related to biogeographical factors and not to the vagaries of collecting effort.

O. nimbus has more specialised protoconch sculpture and penial pilaster patterns than *O. cumulus*. These changes are related to species recognition and indicate a separation earlier than that responsible for the disjunct distribution of *O. cumulus*.

Oreokera nimbus is sympatric with a number of other undescribed charopids but is easily distinguishable by its elevated spire and large size.

The name *nimbus* refers to occurrence of this species on the often cloud enshrouded summit of Thornton Peak and its popular association with *cumulus*.

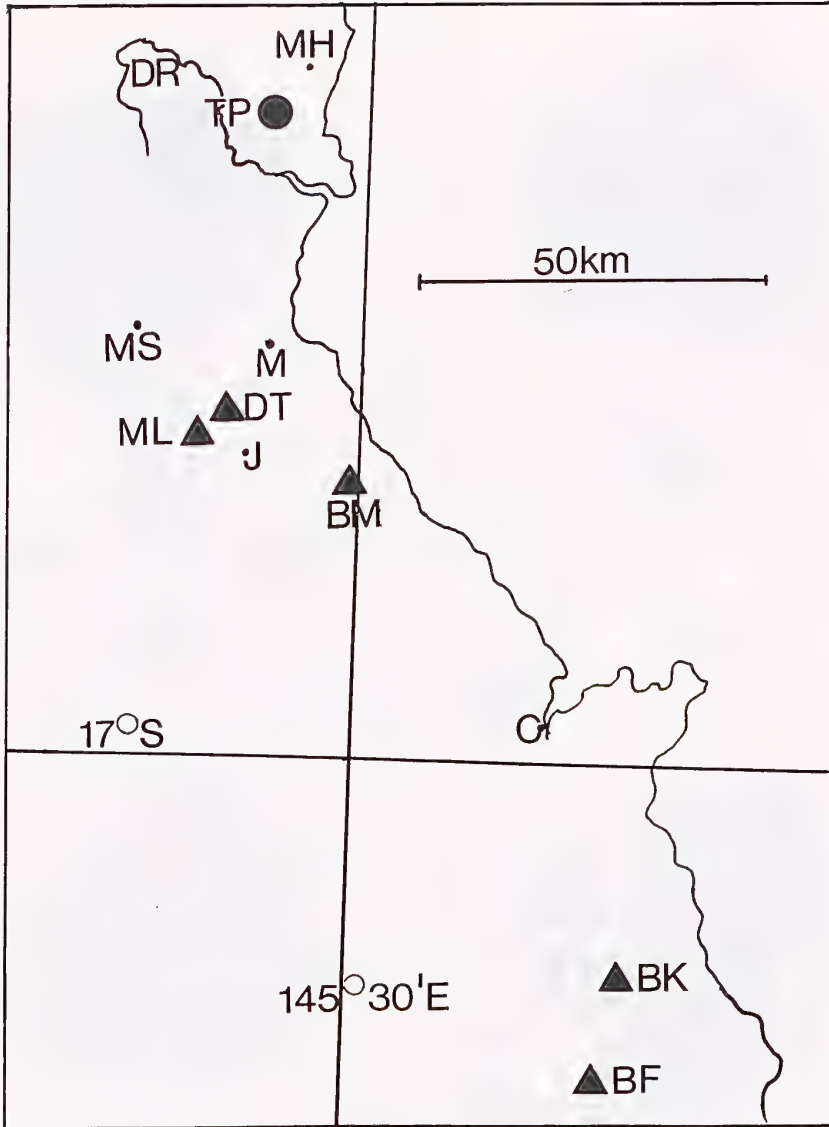


FIGURE 1. Distribution map of *Oreokera cumulus* (black triangles) and *Oreokera nimbus* (black dot) with major landmarks shown.

LEGEND: BF = Mount Bartle-Freer; BK = Mount Bellenden Ker; BM = Black Mountain; C = Cairns; DR = Daintree River; DT = Devil's Thumb; J = Julatten; M = Mossman; ML = Mount Lewis; MH = Mount Hemmant; MS = Mount Spurgeon; TP = Thornton Peak. (Scale as marked.)

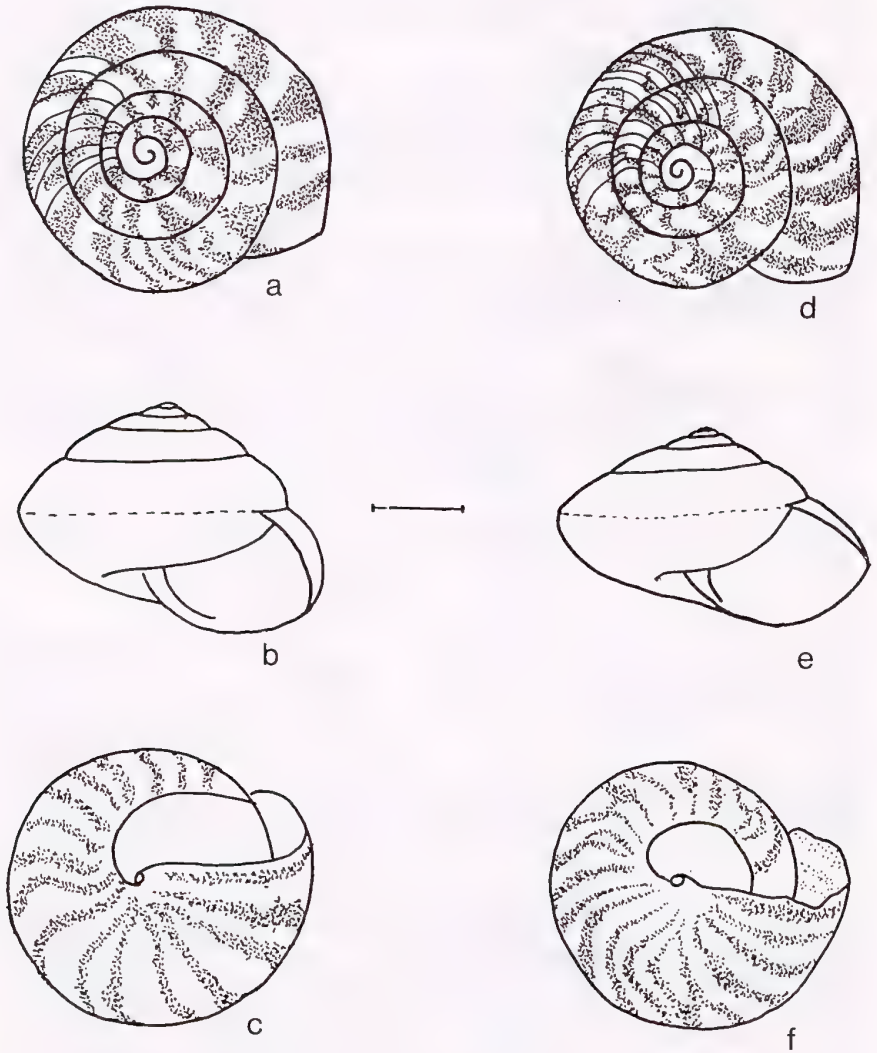


FIGURE 2. Shells of *Oreokera*. (a-c) *Oreokera cumulus* (Odhner, 1917), Mt Bellenden Ker, 1-7 Nov. 1981, QMMO.14765; (d-f) *Oreokera nimbus*, Thornton Peak, 30 Oct. 1983, QMMO.16302, holotype. (Scale line = 2mm.)

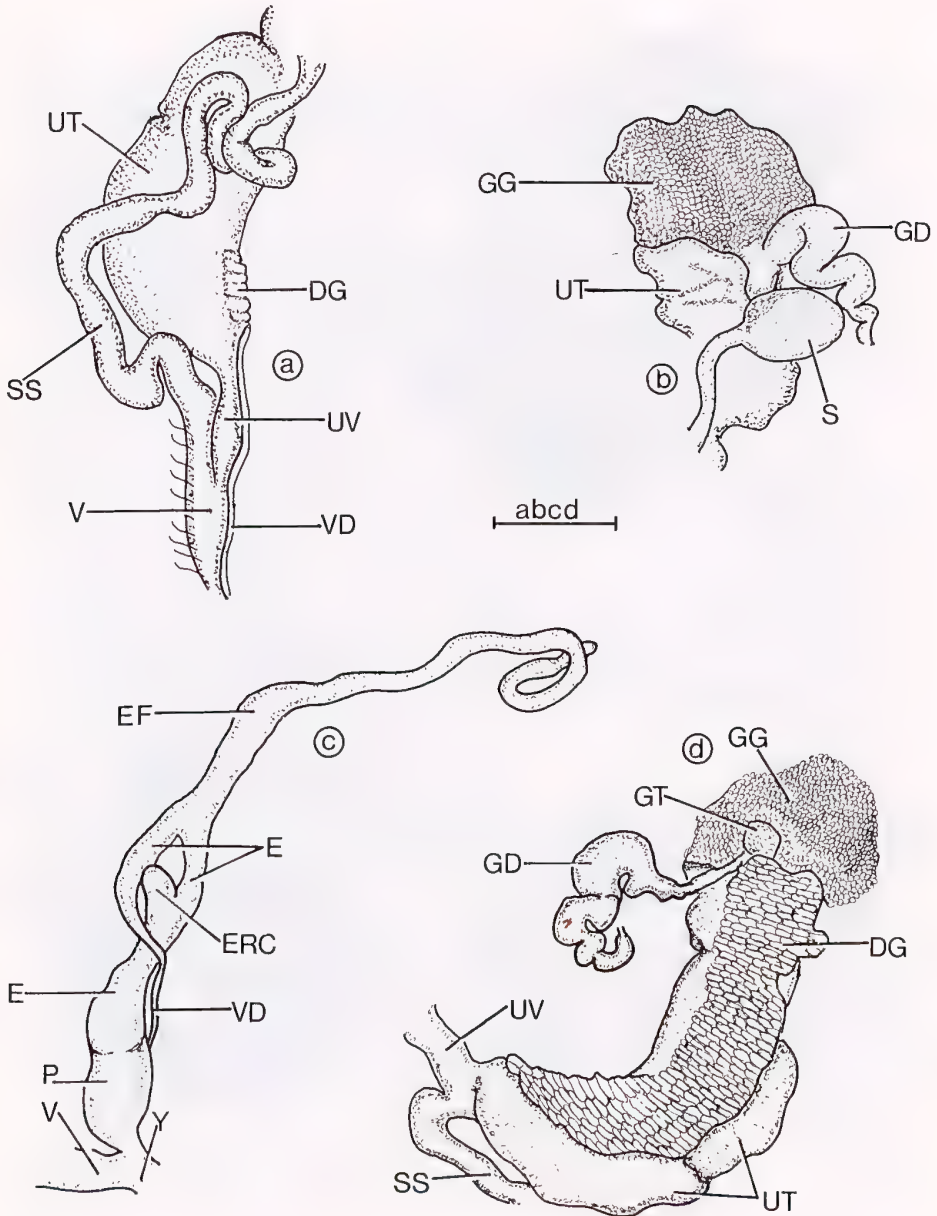


FIGURE 3. Genitalia of *Oreokera cumulus* (Odhner, 1917), Mt Bellenden Ker, 4 Jul. 1983, QMMO.14876; (a) lower female tract; (b) albumen gland, spermatheca and hermaphroditic duct; (c) lower male tract; (d) utero-prostate. (Scale line = 1mm.)

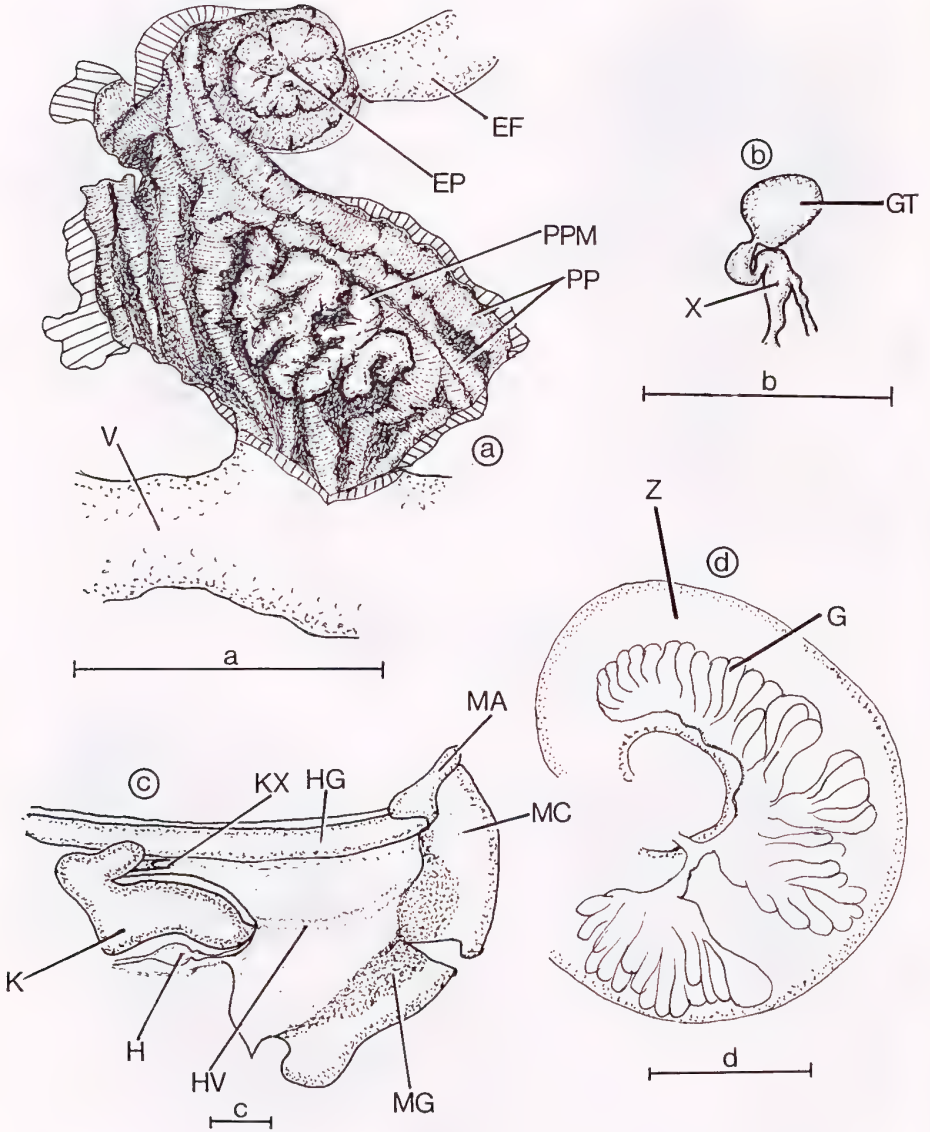


FIGURE 4. Genitalia of *Oreokera cumulus* (Odhner, 1917), (a) Mt Bellenden Ker, 17-24 Oct. 1981, QMMO.11253; (b-d) Mt Bellenden Ker, 4 Jul. 1983, QMMO.14876. (a) penis interior; (b) talon and carrefour; (c) pallial cavity; (d) ovotestis. (Scale lines = 1mm.)

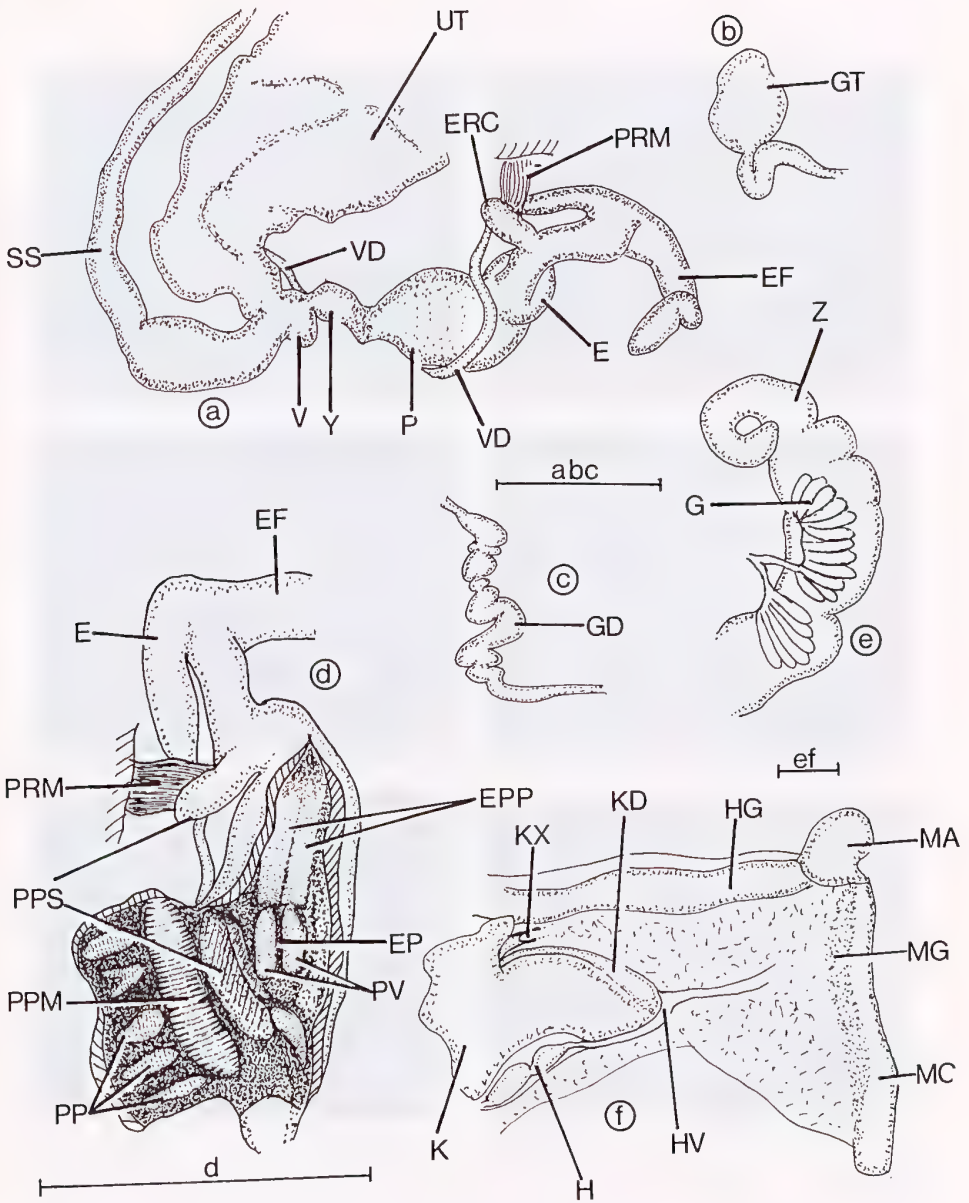


FIGURE 5. Genitalia of *Oreokera nimbus*, Thornton Peak, 30 Oct. 1983, QMMO.15438, paratype. (a) terminal genitalia; (b) talon; (c) hermaphroditic duct; (d) penis interior; (e) ootestis; (f) pallial cavity. (Scale lines = 1mm.)

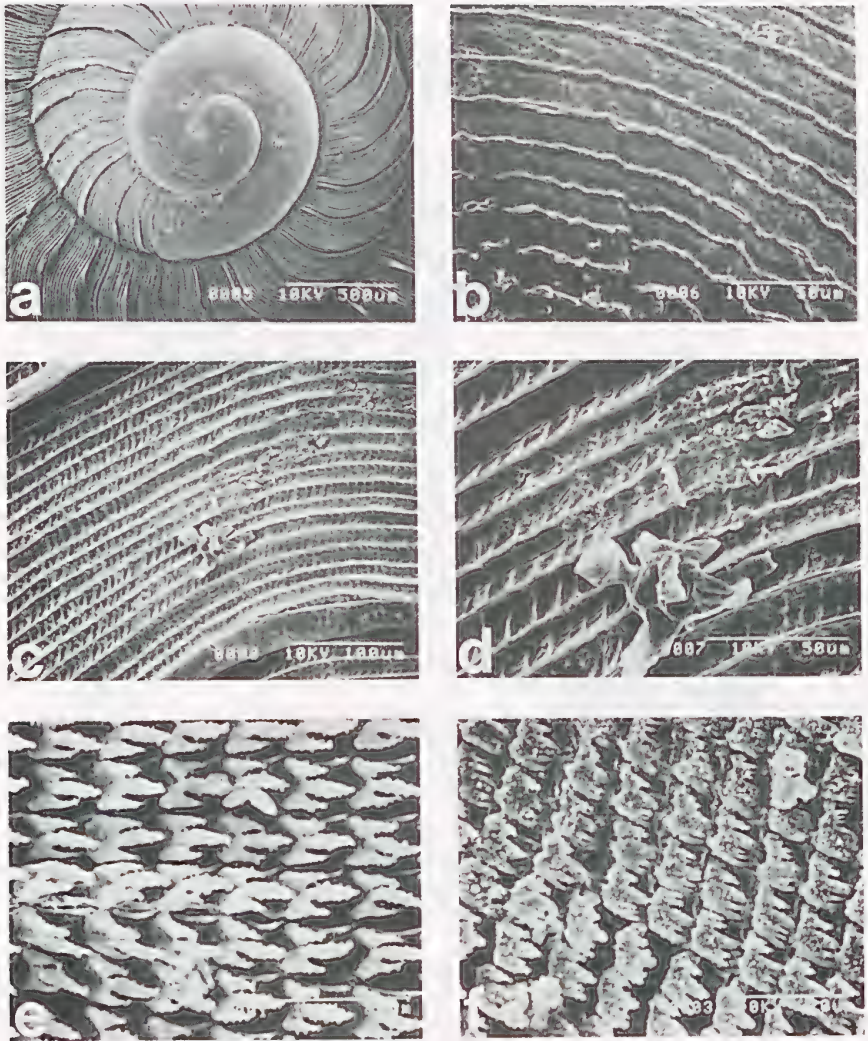


PLATE 1

Shell sculpture and radula of *Oreokera cumulus* (Odhner, 1917), (a-d) Mt Lewis, 9 Sept., 1981, QMMO.15427; (e-f) Mt Bellenden Ker, 4 Jul. 1983, QMMO.14876. (a) apical region; (b) close up of apical cords; (c) microsculpture of first adult whorl; (d) detail of adult microsculpture; (e) central and lateral teeth; (f) marginal teeth. (Scale lines as shown.)

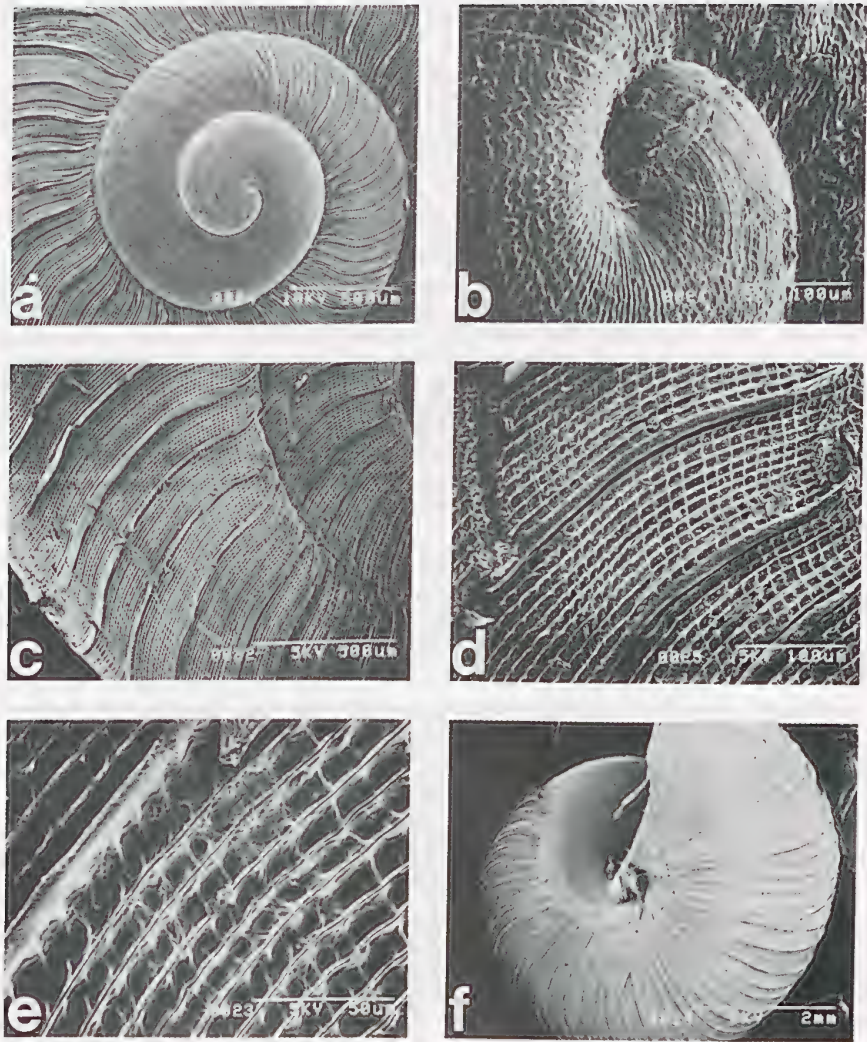


PLATE 2

Shell sculpture of *Oreokera nimbus*, (a) Thornton Peak, 30 Oct. 1983, QMMO.15438, paratype; (b-f) Thornton Peak, 24-27 Sept. 1981, QMMO.15170. (a) apical region: (b) detail of apical cords; (c) adult sculpture; (d) microsculpture on first adult whorl (e) detail of adult microsculpture (f) basal view. (Scale lines as shown).

DISCUSSION

Comparative Analysis of *Oreokera* Patterns

The charopid fauna of tropical and sub-tropical eastern Australia is largely undescribed, while the known taxa of south-east Australia await detailed anatomical study and generic revision. Hence, only a gross outline of the relationships of *Oreokera* can be given at this stage.

Of the recently reviewed Australian taxa (Solem, 1983, pp. 74-81; Solem, 1984; Smith and Kershaw, 1985) only the widespread, minute species, *Discocharopa aperta* (Mollendorff, 1894), and three species from Victoria and Tasmania, *Thyrasona diemenensis* (Cox, 1868), *Stenacapha hamiltoni* (Cox, 1868) and *Mulathena fordei* (Brazier, 1871) are known from soft parts. Two further species *Dupucharopa millestriata* (Smith, 1894) and *Pilsbrycharopa tumidus* (Odhner, 1917), were reviewed known from shells only (Solem, 1984).

In having a much reduced rectal lobe of the kidney (Figs 4c, 5f), *Oreokera* is similar to the widespread *D. aperta* and readily distinguished from the endemic Pacific Island taxa in which the kidney lobes are either equal to subequal in length or the pericardial lobe is significantly shorter (Solem, 1983, pp. 31-32). The New Zealand charopid *Phenacohelix pilula* (Reeve, 1852) and some other east Australian species (Stanisic, unpublished) show similar renal configurations. This feature is also shared with the South American species, *Stephanoda binneyana* (Pfeiffer, 1847). The degree of relationship indicated by this shared character is difficult to assess. Certainly in the case of *D. aperta* the many differences in shell and anatomy between it and *O. cumulus* do not suggest a close relationship. *D. aperta* has a minute white shell with depressed apex, wide umbilicus, reduced whorl count, radially sculptured protoconch and reduced to absent postnuclear spiral microsculpture. Anatomically *D. aperta* has no accessory appendages on the male genitalia, displays sub-apical insertion of the vas deferens, a finger-like talon and more significantly a complete secondary ureter.

Unfortunately, Smith and Kershaw (1985) did not give details of the pallial configurations of *Mulathena fordei*, *Stenacapha hamiltoni* and *Thyrasona diemenensis*, nor did they present some essential fine detail of their reproductive anatomy. While these factors restrict the nature of comparative remarks, sufficient gross differences exist between these taxa and *Oreokera* to indicate strong generic differentiation.

Conchologically, the major difference between *Oreokera* and these species is in the sculpture of the protoconch. The nuclear whorls of *Oreokera* have numerous low, regular to irregular spiral cords (mean 23) whereas *M. fordei*, *S. hamiltoni* and *T. diemenensis* have reticulately sculptured protoconchs in which radial elements predominate and spiral cording may be reduced or absent. Solem (1970, p.262) regarded spiral apical cording in the Charopinae as a primitive condition. It is much more widespread among Pacific Island groups, including the New Caledonian genus *Andrefrancia* Solem, 1960 than Austrozealandic taxa in which patterns of protoconch sculpture show numerous modifications of the three basic patterns — spiral, radial and reticulate.

Pilsbrycharopa tumidus (Odhner, 1917) from the Northern Territory and *Dupucharopa millestriata* (Smith, 1894) from Western Australia show basic departures from *Oreokera* in patterns of protoconch sculpture which highlight the level of experimentation in this feature among Australian taxa. *P. tumidus* has complex apical sculpture consisting of a series of regularly arranged pits while *D. millestriata* has widely spaced radial ribs crossed by unbroken spirals (Solem, 1984).

Among the described sub-tropical and tropical species with spirally lirate protoconchs, *Setomedea seticostata* (Hedley, 1924) from north-east New South Wales and south-east Queensland differs from *O. cumulus* in having a more tightly coiled shell with flattened spire and regularly arranged periostracal setae. *Roblinella disjuncta* Iredale, 1941 from Byron Bay in north coastal New South Wales has a tightly coiled shell with depressed spire, wide umbilicus and poorly defined adult microsculpture. '*Roblinella*' *intermedia* (Odhner, 1917) from North Queensland was incorrectly assigned by Iredale (1937) who believed it had a spirally striate protoconch when in fact the nuclear whorls have strongly reticulate sculpture.

The postnuclear sculpture of *O. cumulus* is typically charopid (Plates 1a, c-d, 2a, c-e) and shows basic consistencies with other Australian and extralimital taxa in having a pattern of primary radials

with a microsculpture of fine radial riblets and spiral cords. However, without adequate scanning electron microscope (hereafter SEM) studies, it is difficult to make meaningful comparisons. Solem (1976, 1983) has shown that optically similar sculpture in the Charopidae and Endodontidae may often be based on quite different microstructure which is only visible through SEM. The New Zealand species *Paracharopa chrysaugaia* (Webster, 1904) and two congeners *P. goulstonei* Climo, 1983 and *P. fuscata* (Suter, 1894) display postnuclear sculpture in which the major ribs develop strong periostacal elements similar to that seen in *O. cumulus*. However these species have quite different patterns of shell shape and highly modified nuclear sculpture. (Climo, 1983). This similarity in sculptural pattern may have a purely functional basis as *P. chrysaugaia* has similar microhabitat requirements to *Oreokera* i.e. under bark of trees.

Anatomically *Oreokera* is distinguished from other Australian, New Zealand and Pacific Island charopids by the presence of two accessory appendages on the male genitalia (Figs 3c, 5a) and lack of a secondary ureter (Figs 4c, 5f). *Mulathena fordei* and *Stenacapha hamiltoni* both lack either an epiphallallic flagellum or caecum. *M. fordei* has no externally differentiated epiphallus while *S. hamiltoni* has a simple epiphallus with more swollen penis. On the other hand *Thyrasona diemenensis* does possess an epiphallallic caecum. Significantly this occurs at the vas deferens — epiphallus junction and apical of the penial retractor muscle insertion. Hence, allowing for the lengthened epiphallus in *Oreokera* this structure corresponds positionally to the flagellum in *Oreokera*. But while Smith and Kershaw (1985) considered the presence of an epiphallallic caecum in *Thyrasona* Smith and Kershaw, 1985 as a diagnostic feature, the phylogenetic significance of accessory genital structures in the Charopidae is difficult to interpret at this stage. The New Guinea species *Pilsbrycharopa gressitti* Solem, 1970 and *Paryphantopsis dauloensis* Solem, 1970 possess epiphallallic diverticula and Solem (1970, p. 263) considered this a major departure from the pattern in Pacific Island charopids. However, both *Pilsbrycharopa* Solem, 1958 and *Paryphantopsis* Thiele, 1928 show a number of basic conchological and anatomical differences from *Oreokera* suggesting that possession of these accessory structures among non-Pacific Island species may be convergent. New Zealand taxa also show some development of accessory appendages but in contrast to *O. cumulus* these diverticula are all penial. Nevertheless, their occurrence in such diverse species as *Maoriconcha oconnori* (Powell, 1941), *Charopa colensoi* (Suter, 1890), *Phenacharopa novoseelandica* (Pfeiffer, 1853) and *Otoconcha roscoei* Climo, 1971 again suggests that they have no phyletic significance (see Climo, 1969, 1970, 1971).

Solem (1983) gives detailed accounts of the variation in the genitalia of 43 species level taxa of Pacific Island Charopidae. *Oreokera* shows significant departures from the basic patterns exhibited by these taxa. The enlarged ovotestis with nearly right angle orientation, strongly kinked hermaphroditic duct, accessory male appendages and epiphallallic insertion of the penial retractor muscle (Figs 3c-d, 4d, 5a) all effectively delineate *Oreokera* from the Pacific Island species. Thus while there are some broad conchological similarities between *Oreokera* and the Pacific Island groups, anatomical differences are sufficient to suggest that these consistencies are a result of parallel evolution over a long period rather than recent common ancestry.

Anatomical similarities do exist between *Oreokera* and some New Zealand taxa. *Thalassohelix propinqua* (Hutton, 1883) has a very similar ovotestis configuration while *Allodiscus dimorphus* (Pfeiffer, 1853) and *Flammulina zebra* (le Guillou, 1812) display kinking of the hermaphroditic duct. In each of these cases however, the features mentioned are the result of secondary modifications due to experiments in visceral hump reduction (*F. zebra*) or size increment (*T. propinqua* and *A. dimorphus*).

Oreokera has an increased whorl count (mean $4\frac{7}{8}$ -) and size (mean diameter 6.36mm) when compared with Pacific Island species (median mean whorl count $4\frac{1}{8}$ -, median mean diameter 2.76mm). It also has increased spire height (Figs 2b, e) associated with the ecological shift to arboreal existence. Hence, the 'radical' patterns seen in the genitalia may be related to associated visceral hump elongation. Certainly the ovotestis orientation and kinked hermaphroditic duct have parallels among large New Zealand species. The lengthening of the epiphallus with the addition of a caecum and extra long flagellum may also be secondary changes associated with the increased shell size and height. That all organs are not involved in this elongation is of no real consequence. Solem (1976, p. 95; 1983, p. 37) has demonstrated that visceral hump compaction or elongation proceeds

on a zonal basis with regard to the organs involved. In this case the elongation has occurred in the 'subterminal' genitalia with no equivalent change in the penis, vagina or pallial gonoducts.

At odds with these seemingly coherent habitat-shift changes are the prominent post nuclear sculpture and conservative foot structure of *Oreokera*. Solem (1976, 1983) found that the larger arboreal and semi-arboreal endodontoid taxa of the Pacific Islands showed reduction or loss of shell sculpture! By way of contrast, Solem and Climo (1985, p. 25) found that New Zealand taxa did not show any correlation between sculptural prominence and habitat. In this respect *Oreokera* fits the New Zealand pattern. The absence of any foot specialisation contrasts with the caudal horn and foss developed in many arboreal New Zealand taxa and may indicate recent utilisation of the arboreal niche under different evolutionary circumstances.

In spite of the many similarities between *Oreokera* and other charopids in the Austrozealandic and Pacific areas, the one feature which distinguishes it from all these taxa is the absence of a secondary ureter (Figs 4c, 5f). Solem (1976, p. 84-87) considered the closed secondary ureter in the Charopidae as a derived condition whose functional significance was largely responsible for the greater evolutionary success of the Charopidae in exploiting habitats where water loss would present a major problem. Hence the Charopidae have had success in arboreal and semi-arboreal situations, survived in desert conditions and produced several lineages of slug-like taxa.

While some Rotadiscinae e.g. *Radiodiscus batricolus* (Guppy, 1868) from Central America (see Baker, 1927, p. 23) have partially complete secondary ureters the absence of a secondary ureter has to my knowledge only been definitely recorded in one other charopid, namely, the Juan Fernandez Island species, *Amphidoxa marmorella* (Pfeiffer, 1845). On the other hand it is the typical condition in the Pacific Island Endodontidae.

Whether or not this entitles *Oreokera* to subfamilial recognition must wait until further studies on the Australian and New Zealand species are completed.

At present the difficulties lie with interpreting the basic patterns to which *Oreokera* should be compared. However, if one accepts the changes which may be due to habitat shift (ovotestis orientation, kinked hermaphroditic duct, epiphallic flagellum and caecum) and those due to species recognition (modified penial pilaster in *O. nimbus*) then the absent secondary ureter, simplified penial pilaster in *O. cumulus* and spiral cording of the protoconch represent a mosaic pattern of primitive characters which may have given rise to the more specialised Charopinae of the Austrozealandic and Pacific Island regions.

Biogeography

The range of *Oreokera* forms part of the largest continuous area of rainforest in Australia. However the actual distribution of the genus encompasses only a select few of the many different structural types of closed forest which combine to make up this rainforest massif. *O. cumulus* and *O. nimbus* are restricted to altitudes above 1000m, and while this may seem unusual, it is a characteristic shared with a number of other biogeographically significant organisms found within this region (see Monteith, 1980).

The humid tropical region of north-east Queensland (lat. 15°-19°S, long. 145°-146°30'E as defined by Tracey, 1982) includes the highest mountains of northern Australia. These mountains (Mt Bartle-Frere, Mt Bellenden Ker, Thornton Peak, etc.) are batholithic granite intrusions of Permian origin, which have become gradually exposed by the erosion of overlying strata. Although not particularly high, the change in altitude from sea level to over 1600m is sufficient to produce a range of microclimates which together with local variation in topography and soil types have led to considerable altitudinal variation in the plant and animal communities existing on these peaks.

Tracey and Webb (1975) mapped the vegetation of the region and showed that the granites and schists of the cloudy wet highlands (greater than 1000m in altitude) supported quite different plant communities to the complex mesophyll vine forests found on the largely basaltic, wet to very wet lowlands and foothills. They recognised two structural types of rainforest at altitudes above 1000m. These were simple microphyll vine fern forest (hereafter SMVFF) and, near the summit, simple microphyll vine fern thicket (hereafter SMVFT). The SMVFT and to a lesser extent SMVFF contain a number of relict plant and animal taxa whose biogeographic status belies the altitudinal

progression of vegetation types from complex to simple. The presence in these montane environments of relict floristic elements such as *Rhododendron lochae*, *Dacrophyllum sayeri*, *Orites* sp. and *Agapetes* sp. attests to their status as major refugia during the Tertiary when many mesic communities underwent large scale attrition (Webb and Tracey, 1981, p. 654).

Kikkawa, Monteith and Ingram (1981, pp. 1707-1712) provide numerous examples of insects which are confined to these refugia. They include both Gondwanic relicts such as flightless dung beetles of the genus *Ignambia* with congeners in New Caledonia and the stag beetle *Sphaenognathus queenslandicus* Moore, 1978, from a genus only otherwise known from South America, as well as autochthonous elements which include the flightless pterostichinine carabid beetles of Darlington (1961a,b,c) and the flightless aradid hemipterans of the genus *Kumaressa* (see Monteith, 1980). These examples highlight the great antiquity of the refugia on the one hand and their role as epicentres of internal evolution on the other. Floristically the situation is analagous with primitive angiosperms and narrow endemics characteristic.

It is in this context that *Oreokera* must be viewed.

With a combination of altitudinally restricted disjunct distribution and primitive characters, *Oreokera* is very much part of this unusual suite of relictual organisms. Monteith (1980) provides a useful summary of some of the non-molluscan elements. In the case of *Oreokera*, its present distribution can best be explained by the fragmentation of a much wider distribution due to habitat regression caused by intermittent episodes of aridity since the mid to late Tertiary. Kershaw (1980) has detailed the chronology of climate induced changes of rainforest communities in the north and has shown that even quite recently (8000 B.P.) there have been major altitudinal shifts of the plant communities in this region. In particular there is evidence to suggest that the present microphyll vine forests of the summits and near summits existed at much lower altitudes in the past when conditions were moister.

Oreokera would certainly have had a more widespread distribution in the past, but is now restricted to the mountain top refugia which ensured its survival through the Tertiary.

It is highly probable that the circumscribed distribution of *Oreokera* in time and space is related to its lack of a water conserving secondary ureter. Solem (1976, p. 100) identified the lack of a secondary ureter in the Pacific Island Endodontidae as a major reason for their restriction to areas of high humidity levels. The lack of a closed secondary ureter necessitates the use of water stored in the pallial cavity to help flush out excretory products. This water loss is a significant problem for small snails. As its moist habitat regressed into mountain top refugia at various times throughout the Tertiary so did *Oreokera*. At present the habitat type is in regression and if this should last for some considerable time then the tendency for the isolated populations of *Oreokera cumulus* (Odhner, 1917) to speciate under localised environmental changes, will increase.

Additionally, the presence of a closed secondary ureter in the Charopidae is considered to be an important factor in the ability of its members to exploit the less humid arboreal and semi-arboreal niches (Solem 1976, 1983). The exceptional case of *Oreokera* (arboreal existence and lack of a secondary ureter) does have analogs within the Endodontidae. Solem (1976, p. 100) reports that species of *Cookeconcha* are found on dead stumps and logs, and under the bark of dead trees. Furthermore, the Tahitian species *Libera bursatella* (Gould, 1846) was taken in the axils of *Freycinetia* at 4700-5000ft elevation. In each case however, the water conservation problem was minimised by high (4375-5000mm/year) rainfall. Thus while *Oreokera* is moist adapted and environmentally restricted, the rainfall is high enough (approx. 5000-6250mm/year) to allow it to exploit niches above the ground stratum. Furthermore, the refugia to which *Oreokera* is now confined would have provided the long term environmental stability necessary for the preservation of this primitive character.

Oreokera nimbus represents an early separation from the antecedent of *O. cumulus*. The vicariant event responsible for this separation was most likely the formation of the Daintree River. Hence *O. nimbus* would have been effectively isolated from even quite recent episodes of rainforest expansion which would have seen present montane refugial communities existing at much lower altitudes and favouring the continued mixing of the *O. cumulus* populations.

The relationships of *Oreokera* remain to be determined, but it would not be surprising to find that these lie with charopids much further south or even in places such as Lord Howe Island, New Caledonia, New Zealand or perhaps South America.

CONCLUSIONS

Oreokera cumulus and *Oreokera nimbus* are ancient relicts which preserve a mosaic of primitive characters. The lack of a secondary ureter in *Oreokera* makes it unique among the Austrozealandic Charopidae and distinguishes it as a taxon with features from which the more specialised Charopidae could have evolved. However, only when further studies on other species in Australia and New Zealand are completed will the implications of this discovery become fully known.

The present distribution of the genus and the events leading to the existence of two species — one widespread and one localised — are inextricably linked to the existence of the montane refugia in which northern mesic communities have managed to persist throughout the climatic vicissitudes of the mid to late Tertiary.

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APPENDIX

List of Anatomical Abbreviations

DG, prostate; E, epiphallus; EF, epiphallic flagellum; EP, epiphallic pore; EPP, epiphallic pilaster; ERC, epiphallic retractor caecum; G, ovotestis; GD, hermaphroditic duct; GG, albumen gland; GT, talon; H, heart; HG, hind gut; HV, principal pulmonary vein; K, kidney; KD, ureter; KX, ureteric pore; MA, mantle lobe; MC, mantle collar; MG, mantle gland; P, penis; PP, penial pilaster; PPM, main penial pilaster; PPS, pocket stimulator; PRM, penial retractor muscle; PV, penial verge; S, spermatheca; SS, spermathecal stalk; UT, uterus; UV, free oviduct; V, vagina; VD, vas deferens; X, carrefour; Z, digestive gland.

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